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Records of Prolonged Diapause in Lepidoptera

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Abstract. Previously unpublished records of diapause and adult emergence one or more years beyond that of other individuals in the species are reported for 19 species of moths in 8 superfamilies. Records of prolonged diapause are summarized, representing 90 species in 10 superfamilies. Prodoxidae, Saturniidae, Pieridae, and Papilionidae predominate, but other taxa may be disproportionately underrepresented owing to lack of study. In Lepidoptera, extended diapause occurs in prepupal larvae or pupae and is most often observed in species that live in areas of seasonal drought and in cone- and seed-feeding species that depend upon crops of erratic abundance. We do not have convincing evidence for a genetically fixed polyphenic expression, wherein a small number of individuals carryover irrespective of environmental conditions.

Prolonged diapause is the maintenance of the dormant state in insects for one or more years beyond the period of emergence by most individuals in the population. There have been many records of the phenomenon in Lepidoptera, particularly in butterflies and Saturniidae, most often originating from pupae held indoors or in climates distant from the natural ones. In the past such records were regarded as aberrant, even astonishing occurrences that had no particular biological significance. Few researchers were sufficiently interested to carry out controlled experimental research on the relationships between the underlying genetic variability and environmental factors that might demonstrate causes and possible adaptive values of prolonged diapause.

In recent years, however, a number of reports suggest that in many insects multiannual delay of development is neither anomalous nor even exceptional and that it may have important adaptive significance (e.g., Danks, 1983; Hedlin et al., 1982; Nakamura & Ae, 1977; Shapiro, 1981; Sunose, 1978; Takahashi, 1977; Tauber et al., 1986). A selective advantage of facultative carryover seems to be especially true in cone- and seed-feeding species that depend upon hosts that produce seed crops of erratic abundance (e.g. Hedlin, 1967; Hedlin et al., 1982; Nesin, 1984; Sunose, 1978) and in desert insects, both phytophagous and predaceous (e.g. Ferris, 1919; Comstock & Dammers, 1939; Linsley & MacSwain, 1945, 1946; Nakamura & Ae, 1977; Powell, 1974, 1975, 1984b, present data).

Twelve years ago I summarized some examples of prolonged diapause in various insects (Powell, 1974), and that paper has been cited several times as though it was a review of the subject, but it is not. Recently two more comprehensive reviews have appeared (Sunose, 1983; Ushatinskaya, 1984). Sunose reviewed my records as well as others and tabulated 64 insect species in which the dormancy has been reported to extend more than a year. Ushatinskaya, evidently unaware of the Sunose compilation, listed a similar number, many of which had not been noted by Sunose. These include eggs of grasshoppers, first instar larvae of parasitic Hymenopera and of tachinid flies that live within sawfly or moth larvae which undergo prolonged diapause, first or last instar larvae of gall gnats, mature larvae of bees, sawflies and meloid beetles, and adults of chrysomelid beetles. In Lepidoptera multiannual dormancy is known only in prepupal larvae or pupae, although in many species diapause occurs in eggs, first or second instar larvae, or adults.

Sunose (1983) listed records of prolonged diapause in 20 species of Lepidoptera, and Ushatinskaya (1984) tabulated 14, of which 10 are additions to Sunose's total. There are a great many more instances known. Probably any lepidopterist who has reared many Papilionidae or Saturniidae is familiar with carryover pupae and emergences of the adults in later years. I have assembled a list of records representing about 90 species, including those reported here (Table 1). These have been reported in more than 60 bibliographic references and several unpublished personal communications. Even excluding the yucca moths (Prodoxidae), which are restricted to North America and for which I have scores of delayed dormancy rearings, about 65% of the records are for Nearctic species. This implies that search of Old World literature has been cursory, and that the phenomenon is known in many more species than I have compiled. In fact, it would be impossible to collect a complete list of references to prolonged diapause because often its records are buried in life history studies, reports on insects of economic concern, or in taxonomic works.

My purposes here are to record previously unpublished instances of delayed emergence in a diversity of moth taxa and to call attention to the likelihood that prolonged diapause is much more prevalent in Lepidoptera than previously supposed. For example, four of the occurrences listed below are species of Pyralidae, Geometridae and Noctuidae. These are families for which I have done only incidental rearing, and therefore one might expect records of extended dormancy to be commonplace in these taxa, yet I have seen few published. This suggests that diapause may be prolonged commonly in these large families, but students have not had sufficient patience to continue surveillance of pupae that do not develop in the first season and to test them in various artificial overwintering regimes. Diapause development is a dynamic process that takes place over weeks or months in North Temperate Zone insects, and the physiological responses to

Table 1. Taxonomic and geographical distribution of some Lepidoptera in which prolonged diapause is recorded

	No. of Species	*Nearctic*	*Palearctic*	*Other*	*Duration (yrs)*
MONOTRYSIA					
Prodoxidae	12	12			2–17
DITRYSIA					
Tineidae	1	1			1
Coleophoridae	2		2		2–3
Gelechiidae	1			1[1]	1.5–2
Ethmiidae	7	6	1		1.5–4
Tortricidae (Olethreutinae)	8	6	2[2]		2–3
Cochylidae	1	1			1
Pyralidae	3	2		1[3]	2–3
Geometridae	5	3	1	1[4]	2–6
Lasiocampidae	1		1[5]		
Saturniidae	18	15	3		1.25–7
Sphingidae	1	1			2
Notodontidae (including Thaumetopoeinae)	5	2	3		1.5–9
Noctuidae (including Agaristinae)	3	2	1		2–4
Pieridae	17	7	10		2–6
Papilionidae	6	4	2		2–6

[1] *Pectinophora gossypiella* (Saunders), diapause recorded in Egypt (Gough, 1916) and Hawaii (Busck, 1917). The species is believed to have originated from the Indo-Australian Region.

[2] Includes *Cydia pomonella* (L.), which probably is introduced from the Palearctic (observed by several Nearctic workers and in Yugoslavia).

[3] *Loxostege frustralis* Zeller (Pyraustinae), recorded in South Africa by Broodryk (1969).

[4] Adults of the Australian species *Arhodia* (?)*retractaria* Wlk. (Ennominae) were reared after 21–23 months in diapause (McFarland, *in litt.*)

[5] Family but no species mentioned by Danilevski (1951) in Russia.

environmental changes are genetically variable. A stimulus that elicits successful development in one species, such as constant chilling for a certain period, may not be effective in another species or another population of the same species from a differing climatic zone or elevation, or even among all individuals within a population.

Typically, prolonged diapause involves some individuals that wait one or more full years beyond emergence of their sibs, in populations in which all individuals enter dormancy, for one of three life cycle patterns: *a*) vernal feeding followed by 9 or 10 months dormancy; *b*) vernal feeding followed by a few months aestivation and autumnal flight, as in *Hemileuca* (Comstock & Dammers, 1937, 1939; Ferguson, 1971), or *c*) facultatively double-brooded populations such as in *Ethmia semilugens* (Z.) (Powell 1974) and *Anthocharis* (dos Passos & Klots, 1969; Shapiro, 1981), so that either a few weeks or nearly a full year in diapause elapses. I also include examples in Tineidae and Cochylidae in which individuals may wait one year even though sibs have emerged within a few days, apparently without undergoing any diapause. The potential for such species to wait more than one season seems likely.

Rearing Methods

Foliage-feeding larvae usually were held in transparent polyethylene bags lined with folded paper toweling to absorb moisture and provide a substrate for cocoon construction. If the host plant material was exceptionally susceptible to excess moisture and decay problems, or the moth species were suspected to use soil for pupation, the lots were placed in translucent plastic boxes or one-gallon tubs with a few cm of sterile sand. Thus natural photoperiod normally was available. Prodoxids were housed in subdued light, in sealed cardboard boxes with a 32–mm emergence aperture at one end. During 1964–1970 most of the initial rearing was conducted in a temperature controlled lab (20–25°C) with variable humidity (RH 38–48% in dry weather, 52–78% during rainy periods). Since 1971, the active larval lots have been handled in a mobile trailer lab on the University of California, Berkeley, campus. Here minimum temperature was controlled (usually 15–16°C) but not maximum, and humidity varied with outside air conditions.

Temperature and relative humidity were recorded continuously by Bendix-Friese hygrothermographs placed on the lab shelving or in temperature cabinets with the collections or in a weather shelter located near outdoor cages. During the emergence season, moths were harvested daily or at 2–3 day intervals. Prodoxids that failed to remain in emergence vials and died inside boxes were harvested at irregular intervals and at the end of each season.

Rearing lot numbers. – A number-letter designation was assigned to each collection of one or more larvae. It reflects the year and month in which the collection was made (e.g., JAP 70C8 refers to the eighth lot recorded in March 1970). The number accompanies all associated material, including reared moths and parasitoids, preserved larvae and other artifacts such as pupal shells, and the data in notebooks. The habitat, hostplant, behavioral, emergence, and preservation data are summarized in a d-Base II program. Voucher specimens and associated data are deposited in the Essig Museum of Entomology, University of California, Berkeley.

Overwintering regimes. – At the end of each season, usually in October or November, lots known or suspected to contain carryover larvae or pupae were exposed to one or a combination of two, storage methods used to manipulate winter temperature conditions:

1. *Laboratory*: A constant temperature (20° ± 1°C), low humidity (40–60% RH) room on the U.C. campus, was used for control sublots in

studies of prodoxids. Other overwintering lots sometimes were left in the mobile trailer lab, which was unheated for 6 weeks in midwinter during 1976–1979.

2. *Berkeley cage*: Many collections were exposed to natural winter temperature and humidity in outdoor screen cages at the Oxford Tract, U.C. Berkeley. Cages were provided with a roof, but in windy storms the containers received direct moisture. Temperatures are moderate at this coastal station, and did not fall below 0°C during several winters monitored. Weekly means of daily maximum and minimum temperatures remained above 10°C during most of the winter. RH fluctuated daily and seasonally, generally between 50–80% in dry weather, 65–95% during storms.

3. *Refrigerator*: A kitchen refrigerator without precise temperature monitor (4° ± 1.5°C) was used for chilling during part of the winter in a few instances.

4. *Russell insectary*: An unheated, fully ventilated lab at the U.C. Russell Reserve near Lafayette, CA, was used to expose prepupal larvae to uncontrolled winter temperatures and humidity. The site is situated ca 10 airline km inland from San Francisco Bay, in the Briones Hills at ca 250 m elevation. Temperatures frequently dropped below freezing and weekly means of daily maxima and minima ranged ca +6°C to 11°C in mild winters, −4°C to +7°C in colder winters. These are much colder conditions than at Berkeley. For example, average monthly mean temperatures at Russell in 1971–73 ranged from 4.5°C lower in October to 8.5° and 7.4° lower in December and January than the 20–year average at Berkeley.

PRODOXIDAE

Prolonged diapause is documented in most yucca moths (Koebele, 1894; Powell, 1984a, 1984b; Powell & Mackie, 1966; Riley, 1892). I have recorded emergences of adults following multiannual dormancy in the prepupal larvae of *Parategeticula pollenifera* Davis, and in nearly all the species of *Prodoxus* and *Agavenema*. Larvae of *Tegeticula* have been observed to survive more than one season; Riley (1892:117) noted that a large percentage fail to complete development in the first year, with some of the moths "not issuing until the second, third of fourth year," but he did not give specific data or report conditions of overwintering. I carried out extensive tests with 4 *Prodoxus* species associated with *Yucca whipplei* in California and *Y. schottii* in Arizona over a 20–year period. The larvae of these species commonly remain in diapause 4–8 years in artificial conditions even though neighbors in the same plant complete development in a prior year. Mass emergence of a whole colony may wait 6 years, if exposed to constant temperature, but mortality was significantly higher as compared to year IV (Powell, 1984a); and in one instance mass emergence occurred after 16 and 17 years in diapause (Powell, 1985, unpubl. data).

Diapause development in *Prodoxus aenescens* Riley and *P. cinereus* Riley is a complex and dynamic process, responding to gradually changing temperatures, probably coupled with moisture factors. Larvae held in constant temperature (± 20°C) and natural photoperiod throughout winter, or exposed to constant temperature chilling (0° to 9°C) for 50 days, remain in diapause, while refrigeration in constant darkness in gradually decreased (6 weeks), then gradually increased (7 weeks) temperatures at means of 3° to 10°C induced varying proportions of individuals to develop (Powell, unpubl. data).

The following records are for species that have not been extensively studied and originate from localities distant from Berkeley, characterized by extremely different seasonal climates from those the larvae were exposed to in rearing.

Prodoxus quinquepunctellus (Chambers)

This species is widespread, from Arizona eastward, in association with an array of yuccas in the Sections Sarcocarpa and Chaenocarpa (Davis, 1967). Larvae were reported by Riley (1892) to sometimes remain in the dry floral stalks 2, 3, or 4 years, although apparently he did not observe successful development of carryover individuals. I obtained delayed emergences of *P. quinquepunctellus* from three collections taken in Arizona and New Mexico, the latter over 4–5 year periods. In contrast to California species of *Prodoxus*, some individuals developed even when held in constant temperature.

The first material, consisting of stalks thought to be two species of *Yucca*, possibly *intermedia* and *glauca*, was collected in late September, 1963, 5 km W of Albuquerque, Bernalillo Co. by J. A. Chemsak (JAP 63J1–J2). A sample of 24 larvae was removed for preservation. The remainder were held in constant temperature through the following two seasons, and diapause development occurred in 7 individuals, one in 1964, 6 in 1965. In November, 1965, half the stalks were transferred to the Russell insectary, where winter III elicited emergence of 5 *P. quinquepunctellus* in 1966. During the same season, the remaining stalks in the lab produced 6 moths; one more emerged from them in 1967. Thus, development of one or more individuals took place each year in the lab, 73% of those that emerged (fig. 1). Moths eclosed in April, 1964, and March to early May in 1965, approximately coincident with the flight period in the Albuquerque area (Davis, 1967).

A second New Mexico collection was made near Portales, Roosevelt Co., in late October, 1973, by N. M. Jorgenson (JAP 73K1), and consisted of current year stalks of *Yucca glauca*. These were held in my lab until December 1, then at the Russell insectary over winter, and 40 *P. quinquepunctellus* responded in diapause development in 1974. In midwinter, 1974–75, a sample of 12 carryover larvae was removed for preservation, and the rest of the lot was moved to the outdoor cage at

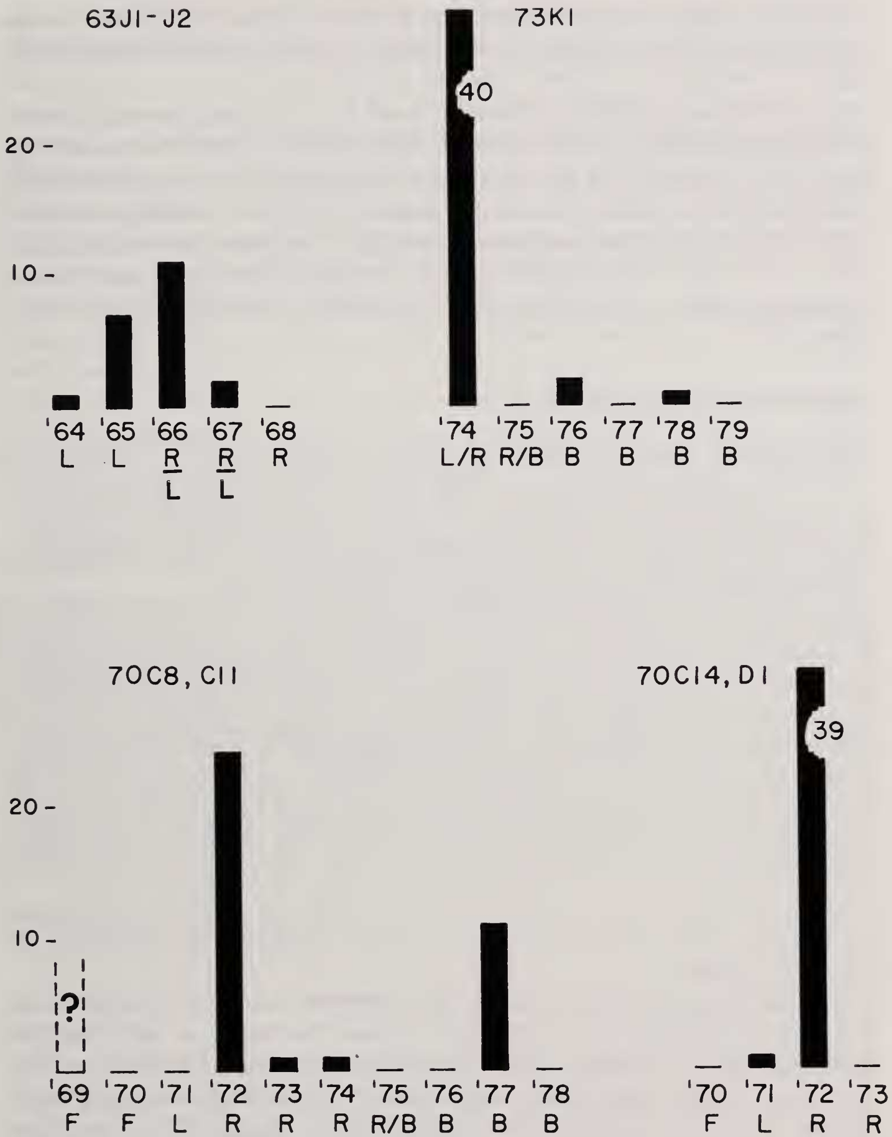

Fig. 1 (upper): Successive annual numbers of *Prodoxus quinquepunctellus* (Chambers) that emerged from two collections of yucca inflorescence stalks (see text for data).
(lower): Successive annual numbers of *Prodoxus coloradensis* Riley that emerged from four collections of *Yucca schidigera* inflorescence stalks from the Mojave Desert (see text for data).
Overwintering sites: F, in field; B, Berkeley, outdoor cage; R, Russell Reserve, unheated insectary; L, laboratory at 20 ± 2°C.

Berkeley, where it was stored for 5 years. Three additional moths emerged, 2 in 1976 and one in 1978, after 3 and 5 years in diapause (fig. 1).

One additional stalk was collected from *Yucca angustissima*, 1 km W of Cottonwood, Yavapai Co., AZ, 30 July 1970, by R. E. Dietz and P. A. Rude (JAP 70G35). It was retained in the lab for one year, during which no moths emerged, then transferred to the Russell insectary. There 26 *P. quinquepunctellus* successfully completed development, 30 May to 20 June 1972, following the second winter. Only one flaccid-appearing larva was discovered by splitting the stalk at the end of 1972.

Prodoxus coloradensis Riley

This species feeds in stalks of *Yucca schidigera* and *Y. baccata* in California and in other yuccas of the Section Sarcocarpa in the western U.S. (Davis, 1967). Collections made in the Mojave Desert, 31 March – 2 April 1970 (Dietz & Powell), indicated that prolonged diapause in natural populations is commonplace in that habitat.

At a site 8.5 km north of Cottonwood Springs, Joshua Tree National Monument, Riverside Co., CA, *Y. schidigera* was in full to late bloom on March 31, and none was seen with newly emerging inflorescences. *P. coloradensis* adults were numerous, yet there appeared to be no 1969 stalks. Dry stalks in the vicinity appeared to originate from 1968; each had emergence holes along with few to many carryover larvae (JAP 70C7–8). Because adults of *P. coloradensis* had already emerged, it could not be inferred with certainty that the observed stalks were older than one year. It was evident, however, that either a substantial portion of larvae had carried over from 1968 or a previous season, or that many 1969 larvae had not completed diapause development for the 1970 season.

At Belle Campground, 32 km to the northwest and 300 m higher than Cottonwood Springs, *Y. schidigera* showed no signs of inflorescence development. Flowering and yucca moths had been observed at this site in mid-April, 1963, and it was evident that activity would not begin before mid to late April in 1970. Again, there appeared to be no 1969 stalks, while those from a previous year contained old emergence holes along with carryover *Prodoxus* larvae (JAP 70C11), which tended to confirm our estimate of stalk age at Cottonwood Springs. On the basis of weathered appearance of the stalks, subsequent vegetative growth, and lack of prior emergences, *Y. schidigera* stalks at Ryan Mountain, Joshua Tree Natl. Mon. (JAP 70C14) and Cedar Canyon, 27 airline km NE of Kelso, San Bernardino Co., CA, (JAP 70D1), also were judged to be more than one year old.

The 1970 collections were housed at the Russell insectary beginning in early April, and no *P. coloradensis* emerged in 1970, nor in 1971 after transfer to the constant temperature lab over winter 1970–71. Most moths (82%, n=78) completed development in 1972, following their first overwintering at the Russell insectary. Additional larvae were discovered in 70C11 in February, 1974; the lot was retained and exposed to winters in the cage at Berkeley. Only 2 adults completed development in the succeeding 2 years, then, inexplicably, 11 *P. coloradensis* (38% of the Belle Campground total, n=29) emerged in April 1977, following a second full winter of drought conditions in Berkeley, 9 years after their larval feeding in 1968 stalks (fig. 1).

It is possible that the 70C14 and 70D1 collections, which originated from higher or more northern sites than Belle Campgound, were made sufficiently early (e.g., 4 or 5 weeks ahead of flowering) that development was interrupted; but negative results of all other 1970 collections including those of *P. sordidus* Riley (see below) and *P.* y-*inversus* Riley (Powell, 1985) suggested that the 1969–70 winter was one that failed to elicit diapause development in Mojave *Prodoxus* generally.

Evidence of 1969 failure in the *Y. schidigera* inflorescence crop was dramatic at a site on Black Canyon Road, south of Cedar Canyon. Here an extensive stand of tree-like *Y. schidigera* possessed 1969 stalks that were dry, hard, and black, atrophied before they were fully grown, as though they were killed by a late freeze. None had any signs of lepidopterous larval feeding. A number of 1968 stalks were found containing small numbers of larvae; some had emergence holes left by sibs that must have faced catastrophe in 1969. A collection (JAP 70D4) of the pre-1969 stalks produced no adults in 1970 and only one *P. coloradensis* in 1972 after overwintering at Russell. Dissections of the stalks in early 1973, however, revealed a few larvae still in diapause.

Prodoxus sordidus Riley

Moths treated under this name are believed to represent two species (D. S. Frack, *in litt.*) associated with Joshua Tree, *Yucca brevifolia*. It appears that a species with tan forewings feeds in the inflorescence scapes, while a whitish moth originates from larvae in pods. However, some of my stalk-inhabiting larvae produced the pale morph, and more information is needed to confirm separation of larval feeding niches of the two. My rearing data are pooled.

Collections at Antelope Valley, 33 km E Gorman, Los Angeles Co., CA, March 11, 1963 (Chemsak & Powell, JAP 63C8) just ahead of the current season flowering, confirmed that prolonged diapause occurs – most emergences took place in late March and early April, 1963, but 2 *P. sordidus* completed development in February, 1964 after storage in the lab. A midwinter collection from 5 km SE Pinon Hills, L. A. Co., 23 December 1969 by P. A. Opler (JAP 70A1) produced only 6 adults after housing in the lab for the remainder of the season. None emerged in 1971 after winter II in constant temperature, but in 1972, 90 moths responded to winter III at the Russell insectary. Three more individuals waited until 1973, following a second winter at Russell, and one *P. sordidus* emerged in the 6th season, after the material was transferred to Berkeley in midwinter 1973–74.

The same emergence pattern was shown by population samples made 31 March – 2 April 1970 in the central Mojave Desert, despite the fact that they were collected after a full winter in the field. One of these (JAP 70C12) at Belle Campground, Joshua Tree Natl. Mon., Riverside Co., CA, was made while *Y. brevifolia* was in full bloom and *Prodoxus* was active in low numbers. It was not possible to judge stalk age precisely, but it appeared at least two seasons growth contained larvae in diapause; none of these matured in 1970. Three more collections were made at higher, more northern sites, ahead of 1970 *Y. brevifolia* flowering (70D2: Cedar Canyon, 27 airline km NE Kelso, San Bernardino Co., CA; 70D10: 6 km S of Barnwell, 44 airline km NE Kelso; 70D24: Kyle Canyon, 15 km W Highway 95, 30 airline km WNW Las Vegas, Clark Co., NV). In each sample, no *P. sordidus* matured in 1970, nor in 1971 following a year in the constant temperature lab. Most of the emergence (84%, n=140) occurred in year III following overwintering at the Russell insectary in 1971–72, while 6 individuals eclosed in each of the next two years after another winter at Russell and at Berkeley from midwinter 1973–74. Only one of the collections (70D10) was retained beyond the 5th year, and 10 *P. sordidus* developed successfully in 1975 after storage over winter in the outdoor cage at Berkeley, but none matured in the 7th season (fig. 2).

Prolonged diapause would seem less critical to continuity of populations in *P. sordidus* than in other *Prodoxus* because *Yucca brevifolia* blooms more consistently. Nonetheless, combined with observations of *P. coloradensis*, the data indicate that certain winters are suboptimal to diapause termination in *Prodoxus* in widespread areas of the Mojave Desert.

Weather records from Twentynine Palms (15 airline km N of Belle Campground, at 610 m) and Mountain Pass (35 air km NNW of Cedar Canyon, at 1450 m) for the preceding 4 and 3 years, respectively, showed that the 1969–70 winter was unusual, if not exceptional in a long-term sense. At both stations the rainfall total for October through March was lower than in any of the preceding few years, 19 mm contrasted to a 5–year average of 45 mm at Twentynine Palms, and 50 mm vs. a 4–year average of 92 mm at Mountain Pass. Possibly of greater significance to the moths, the 1969–70 winter was characterized by unusually mild temperatures. In the 13–week midwinter period, December through February, monthly means averaged 11.1°C at Twentynine Palms in 1969–70, contrasted to a range of 8.5–10.9° (avg. 9.9°) during the preceding 4 winters; while at the higher station monthly means averaged 7.0°C in 1969–70, but ranged 3.1 to 6.7° and averaged only 4.8° during the preceding 3 seasons.

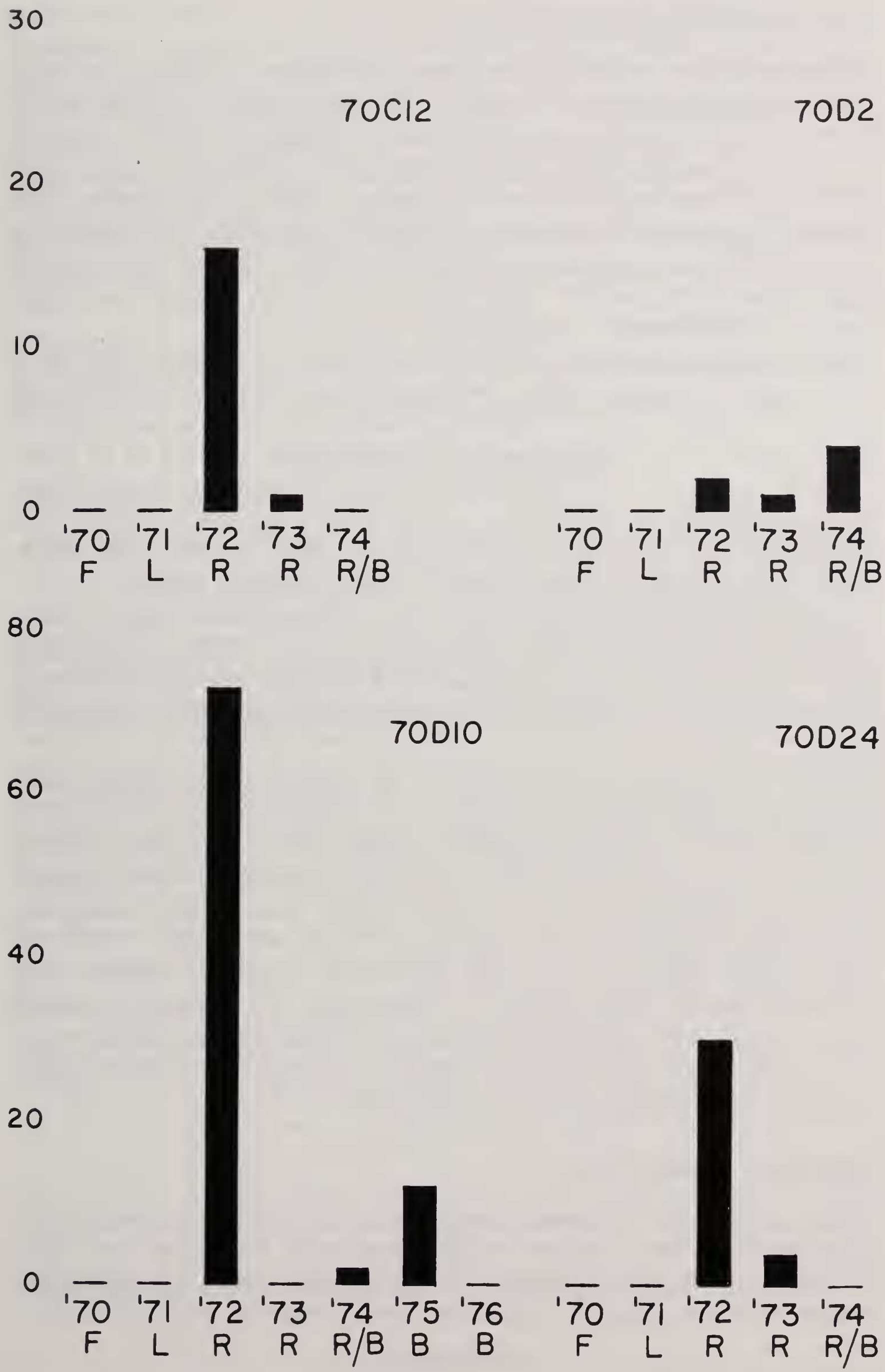

Fig. 2: Successive annual numbers of *Prodoxus sordidus* Riley that emerged from four collections of *Yucca brevifolia* inflorescence stalks from the Mojave Desert (see text for data). Overwintering site designations explained under figure 1.

Agavenema barberella (Busck)

Agavenema species feed on *Agave* and display larval habits similar to those of stalk-inhabiting *Prodoxus*. The adults are not found in the flowers of the larval host, as are *Prodoxus*, and larvae usually occur in the main scape well below the inflorescence. Collections were made from various species of *Agave* in Arizona in 1968–1970. Stalks were housed at the Russell insectary in 1968–69 and 1969–70 winters, in the lab 1970–71, returned to Russell in 1971–72 and not retained beyond the fourth season. Development occurred irrespective of the kind of artificial winter conditions.

Lots collected at Madera Canyon, Santa Rita Mts. in June 1968, prior to the current season flight, from *Agave palmeri* (JAP 68F43–44) (Opler & Powell), produced moths primarily the same season (83% of those reared, n=130). Emergences occurred from 15 July to 13 October, and 20 larvae were harvested in late September. Only 7 individuals completed development in 1969, after exposure to winter II at the Russell insectary, followed by none in 1970 and 1971, yet 15 *A. barberella* emerged in the 4th season after storage at Russell.

Larvae were collected in *Agave schottii* at Molino Basin, Santa Catalina Mts., in September, 1969, after the summer activity period (JAP 69J10). Small numbers of moths issued, 5 in 1970, 3 in 1971 (following a lab winter), and 7 in 1972, after winter III at Russell (47% of the total, n=15).

Lastly, 7 collections of one-year old or current season stalks were made from 3 *Agave* species in central and northern Arizona,[1] 29 July to 2 August, 1970. All yielded similar results: one or no moths in 1970, modest numbers in 1971 (19% of the total reared, n=134), despite having overwintered in the lab, followed by most of the emergence (78%) in the 3rd season after exposure to winter at Russell in 1971–72.

The normal flight period of *A. barberella* is poorly known, with scattered records from March to September in southern Arizona (Davis, 1967). The flowering phenology of most agaves probably enables a more protracted activity season by *Agavenema* within populations than is characteristic of yucca moths.

Agavenema pallida Davis

This species, which is closely related to the preceding one and may be a geographical race, occurs in the deserts of California and Baja California Norte, Mexico (Davis, 1967; UCB specimens). Its seasonality is more restricted than that of *A. barberella*, similar to the California

[1]JAP 70G30: 4 km E of Peach Springs, Mohave Co., 1969 stalks of *Agave utahensis*; 70G31: same data, 1970 stalks; 70G32: 5 km SW Mingus Mtn. summit, Yavapai Co., 1969 stalks of *A. parryi*; 70G33: same date, 1970 stalks; 70G36: Molino Basin, Sta. Catalina Mts., Pima Co., 1969 stalks *A. schottii*; 70H6: same data, 1970 stalks; 70H5: 1.5 km NE of Colossal Caves, Pima Co., 1970 stalks *A. schottii* (R. E. Dietz, J. Powell and P. A. Rude).

species of *Prodoxus*. Collections from *Agave deserti* in March, 8 km E Jacumba, San Diego Co., CA (JAP 63C31) and April, 1963, Pinyon Flat, 29 airline km SE of Idyllwild, Riverside Co., CA (JAP 63D10) revealed prolonged diapause. Carryover larvae remained at the end of the season, and in 63D10 a few adults emerged in 1964 and 1965 despite housing in the lab during the preceding winters.

Two collections made in Baja California in March, 1972 and 1973, yielded *A. pallida* adults in diminishing numbers in years I, II, and III. A total of 25 moths emerged in year I following overwintering in the field (51%, n=49), 17 in year II (35%), and 7 in year III (14%), and 2 carryover larvae were discovered in winter IV (JAP 72C12: 8 km E of El Rosario, 1971 stalk of *Agave shawii*; 73C5: 5 km S of Rancho Santa Ynez, 1972 stalks of *A. cerulata* spp. ?*nelsoni*; Doyen & Powell).

TINEIDAE: SCARDIINAE

"Scardia" cryptophori (Clarke)

This large gray tineid is widespread in montane western North America. It was transferred from *Morophaga* H.-S. to the genus *Scardia* Tr. by Davis (1983), who treated *Morophaga* and its Palearctic type species as a synonym of *Scardia*. However, *S. cryptophori* is structurally and biologically dissimilar from Nearctic members of *Scardia*. In contrast to other Scardiinae and other fungus-feeding Tineidae, this species is host-specific, feeding in the sporophores of *Polyporus* (*Cryptophorus*) *volvatus*, which grows on recently dead conifers (Lawrence & Powell, 1969). This fungus is available throughout the season but appears to be in a fresh state preferred by *S. cryptophori* primarily in spring following winter precipitation and snow melt.

Among numerous collections from the Sierra Nevada and Cascade Ranges in California, two from Trinity County produced some larvae that proceeded to maturity without dormancy, as most do, and others that entered diapause for one year. This suggests that adverse conditions, particularly desiccation, may prolong diapause.

Four collections of sporophores were made in the vicinity of Hayfork, Trinity Co. in late May, 1973. Moths (n=36) emerged from all 4 lots 15–25 June, but in two groups (JAP 73E46, E47) a number of larvae spun cocoons in dry spots remote from the fungus, and most of these did not emerge. A few cocoons were cut open in September, revealing carryover prepupal larvae. The lots were stored in boxes at the Russell insectary. After removal to Berkeley in early June, 1974, 10 *M. cryptophori* emerged in late June, one year later than their sibs.

ETHMIIDAE

Ethmia plagiobothrae Powell

This species flies in early spring, primarily in March, in the foothills of the Coast Ranges and Sierra Nevada in California. The larvae feed on flowers of *Plagiobothrys* (Boraginaceae) a spring annual, and pupae remain in diapause from the beginning of the dry season until early spring the following season. I have made numerous collections of larvae, but they are highly susceptible to disease in rearing, and the few adults obtained emerged after one year (Powell, 1971). In one instance (JAP 69D58, Powell, 1971) 10 *E. plagiobothrae* were reared after one winter (100% of the emergence) even though the collection data and rearing conditions were essentially the same as for a collection of the closely related species, *E. scylla* Powell, that produced moths 2, 3 and 4 years after pupation (Powell, 1974). In another collection (13 km SE Three Rivers, Tulare Co., 4 May 1979, JAP 79E24) all 4 adults emerged the next year, between Feb. 14–27. On two occasions, however, pupae were still healthy appearing during the second winter, after 19 and 21 months, but development did not take place (Powell, 1971). Thus it was not surprising that a collection in 1980 produced one *E. plagiobothrae* that delayed until the second spring before emerging.

We found larvae on *Plagiobothrys nothofulvus*, 6 km S of Rough and Ready, Nevada Co., CA, on 4 May 1980 (M. Buegler, J. DeBenedictis & Powell) (JAP 80E17). About a dozen were placed in pill boxes, 2 to a container with inflorescences and folded tissue paper. After cocoon construction the boxes were left open inside a translucent plastic box, stored in the mobile trailer lab at Berkeley through the summer. In October they were moved to the outdoor cage, but no development resulted after the first winter. In 1981–82 the material was again exposed to winter in the cage, and one male emerged between 24 February and 24 March, 1982. Other individuals were unsuccessful in pupation, succumbing either to disease or desiccation prior to or after cocoon construction.

Ethmia epileuca Powell

This species was described from the Panamint Range, CA, in the northern Mojave in 1959 and subsequently has been recorded in the low deserts of southern California, Baja California, and Arizona (Powell, 1973; UCB specimens). The foodplant, an annual *Phacelia*, was discovered in 1977, and the one specimen reared spent two years in diapause.

A few *Ethmia* larvae were found feeding externally on *Phacelia crenulata* (Hydrophyllaceae) at Zzyzx Springs, near Baker, San Bernardino Co., CA, 20 April 1977 (JAP 77E94). They were provided with soft paper toweling, but only one *E. epileuca* successfully constructed its cocoon. It was stored in a transparent plastic bag in the mobile trailer lab through summer and fall, then in an outdoor cage at Berkeley during late winter and spring, 1978, but diapause development did not occur. The cocoon was again placed in the cage for the 1978–79 winter until mid-February, then in the mobile lab. A female

E. epileuca emerged on 2 April 1979 after nearly 24 months in diapause. The 1978–79 winter was appreciably colder than the preceding year at Berkeley, 190 heating day degrees greater (based on 18.3°C), during October through February.

Interestingly, a related species, *E. semilugens* (Z.), which has the capability of developing with a short diapause of a few weeks, of one year, or of several years (Powell, 1974), also feeds on *Phacelia crenulata* (Powell, 1971). Collection records for *E. epileuca*, however, indicate that this species has a univoltine cycle with flight in early spring.

Ethmia (Macelhosiella Group) n. spp. A, B

Larvae that proved to be two undescribed species which are structurally and biologically similar to *Ethmia geranella* (B. & Bsk.) were discovered in western Fresno County, CA in March 1975 and collected again in April 1978. Both species feed in spring, estivate as pupae, and fly in late fall, as do other members of the Macelhosiella Group. Eggs hibernate, presumably in diapause or a temperature-dependent quiescence (Powell, 1973). In both Fresno County collections, some individuals carried over to a second or subsequent autumn; however the pattern was quite different between the two species, even though they were reared and held over winter in identical conditions.

Species A: The larva is green with faint longitudinal, gray integumental shading. The adult is a whitish moth with faint ochreous along the discal cell, and it differs from other western species of the group by lacking a hindwing costal penicillus in the male. P. A. Rude and I collected larvae on *Phacelia tanacetifolia* (Hydrophyllaceae) at the Ciervo Hills, 29 airline km SE of Mendota, Fresno Co., CA, 16–18 March 1975 (JAP 75C1) and at Jocalitos Cyn., 9 airline km S of Coalinga, Fresno Co., 17 March 1975 (JAP 75C2). Larvae were placed in translucent plastic vials and cardboard pill boxes, 1 or 2 per container, with folded tissue and small blocks of yucca scape pith, into which they burrowed for cocoon construction. Others were confined in translucent plastic bags with paper toweling and hostplant material. They were stored in the mobile trailer lab at Berkeley for the remainder of spring and early summer; in late July about half the containers were moved to the Russell insectary, while the remainder were placed in the outdoor cage at Berkeley in September.

Most of the moths (n=25) emerged in October, 1975. The carryover cocoons were exposed to winter conditions at Russell during January – April, 1976, and subsequently were retained in the outdoor cage at Berkeley. Two adults completed development in October, 1976, and 13 others developed but were trapped in the cocoons and unable to distend the wings, probably in the first season. No more emerged in 1977 or 1978.

In early April, 1978, following the 1975–77 drought, Jocalitos Canyon was again a sea of wildflowers, and we made additional collections of the two *Ethmia*. Larvae of Species A (78D12) became diseased and most were preserved for taxonomic study; 7 were retained in translucent plastic boxes with paper toweling and yucca blocks in the mobile trailer lab. Four of these emerged as adults 25–30 October 1978. The remaining 3 carried over and eclosed 10–27 Oct. 1979, after storage over winter in the outdoor cage at Berkeley.

Thus 29 of 34 successful emergences (85%) of Species A occurred during the first fall after larval feeding, while the remainder developed one year later.

Ethmia Sp. B: The larva is irregularly mottled, predominately gray, with longitudinal bands of orange dorsally and laterally, resembling that of *E. charybdis* Powell (Powell, 1971). The adult is dark gray; the forewing has a trace of ochreous and a variable black line along the discal crease and a whitish dot at the end of the discal cell, and the male hindwing has a costal penicillus. Thus the adult is structurally quite similar to that of *E. timberlakei* Powell, which feeds on *Phacelia ramosissima* in southern California, but the larva of the latter is green with a yellow dorsal stripe (Powell 1971). Larvae of Species B were mixed with those of Species A in the field at Jocalitos Canyon in March, 1975, but were outnumbered ca. 10:1. I could not detect a spatial differentiation on the plants; both fed within the scorpioid floral spikes. In the lab, larvae were segregated by color and handled in the same rearing conditions as outlined for Species A.

In marked contrast to the preceding species, no individuals of Species B completed development in 1975. Instead, all 4 moths that metamorphosed did so after carrying over, two in early November, 1976, and one each in November 1978 and 1979. The same diapause behavior obtained in the April 1978 collection at Jocalitos Canyon: about a dozen larvae were confined, of which none developed in 1978, 2 moths emerged in October 1979, none the following year, and 2 more in October, 1981, after 42 months in diapause.

I visited the Jocalitos Canyon site on 21 March 1977, following two drought years in California, and found the spring vegetation dry; there had been essentially no germination of annuals. Hence, a large larval eclosion of *Phacelia*-feeding *Ethmia* would have been mostly doomed, and if prolonged dispause in the pupal stage acts as a buffer against such disasters, the strategy must be keyed to maintenance of diapause through autumn preceding a dry spring.

Adults of Species B were taken at blacklights at Jocalitos Canyon on 10 November 1977 (Powell & Rude). There had been no heavy rains in the region that fall, only ca 6 mm in the Fresno area, less than 1/4 the normal, by early November; the drought did not end until late November and December, 1977. This leaves unanswered the question of how prepupal larvae appraise the potential for spring growth of annual *Phacelia* and either maintain diapause or undergo development in October.

TORTRICIDAE: OLETHREUTINAE

Grapholita vitrana (Walsingham)

Grapholita vitrana was originally described from northern Oregon, and it is commonly associated with *Astragalus* (Fabaceae) in sandy situations along coastal areas of California, on San Miguel and Santa Catalina Islands, and in interior and coastal areas of Baja California, Mexico, including Isla Cedros (SDNHM, UCB Specimens). The larvae feed on green seed in the bladder-like pods of locoweed.

A collection of pods containing larvae of *G. vitrana* and *Everes amyntula* (Bdv.) (Lycaenidae) was made from an *Astragalus* growing on riverine dunes along the Salinas River near King City, Monterey Co. on May 3, 1974 (JAP 74E20). The butterflies emerged within a month, while the tortricids spun tough, papyrus-like cocoons in which prepupal larvae entered diapause. After drying, the lot was stored in the mobile trailer lab on the Berkeley campus. Seven *G. vitrana* emerged between 28 March and 28 April, 1975. The remaining cocoons were left undisturbed and in the same overwintering conditions except without heat control for 5 weeks in December and January, 1975–76, so were exposed to temperatures of 2° to 4°C on several occasions. Diapause development occurred in 4 individuals (2♂, 2♀), and moths eclosed between 23 March and 11 May 1976. Similar housing of remaining carryover larvae during the third winter, 1976–77, resulted in 5 more *G. vitrana* (2♂, 3♀) emerging, between 26 February and 17 April, 1977, after 33–35 months in diapause.

Diapause extending to a second or third year has been recorded in several other seed-feeding species of *Grapholita* and the closely related genus *Cydia* (e.g., Dickson, 1949; Hedlin, 1967; Nesin, 1984; Tripp, 1954).

COCHYLIDAE

Cochylis yuccatana (Busck)

This distinctive species is widespread in the southwestern deserts, from Texas (TL: Nuecestown) to southern California and Baja California Norte, Mexico (UCB Specimens). The type series was reared from *Yucca baccata*; we have found the larvae in flowers of *Yucca brevifolia* in the Mojave Desert, and *Agave shawii* in coastal Baja California Norte. There are no records of multiannual diapause, but the species is capable of either completing development without delay or remaining dormant until the following year, which suggests a potential for prolonged diapause exceeding one year.

A single larva taken 5 km W of Palmdale, Los Angeles Co., CA, from *Yucca brevifolia* in late March, 1968, pupated and produced an adult 15 days after collection (JAP 68C62). Several caterpillars feeding on *Agave* near San Telmo, Baja Calif., in mid-March, 1972, did not mature that spring, but two moths eclosed in late April, 1973, after 13 months in diapause (JAP 72C6); while another collection from the same host near El Rosario, Baja Calif., in late March, 1973, produced larvae of both types. Five *C. yuccatana* emerged between 24 April and 8 June, 1973, and one later that summer, and one prepupal larva carried over to complete development in May or June, 1974 (JAP 73C4). Both carryover lots were housed at the Russell insectary.

PYRALIDAE: CHRYSAUGINAE

Satole ligniperdalis Dyar

This curious polymorphic and sexually dimorphic species is widespread in the southwestern Nearctic, from western Texas to the western edge of the deserts in California (TL = Portal, AZ). Adults have been reared from seed pods of *Chilopsis linearis* (Bignoniaceae) in southern Arizona and southern California (USNM specimens).

A collection of the linear fruits of *Chilopsis* was made by J. T. Doyen on the Kelso Dunes, ca 12 airline km SW Kelso, San Bernardino Co., CA, on July 14, 1974 (JAP 74G9). Ten adults of *S. ligniperdalis* emerged between 18–27 July, and two more later that fall. Although several larvae abandoned the pods by late July and the plant material became badly covered by sooty mould, an apparently healthy larva was revealed by dissecting its cocoon in February, 1975. The lot was therefore placed in a cardboard box and stored in the outdoor cage at Berkeley. Two females emerged in early September, 1975, one on June 25, 1976, and a final one in the fourth season, between October and December, 1977, after 38–40 months in diapause.

Evidently larvae were fully fed at the time of collection and spent diapause as prepupal larvae in cocoons. Because they were held in subdued light and the emergence dates varied by more than two months after late June, it appears photoperiod was not a primary factor influencing diapause development.

PYRALIDAE: CRAMBINAE

Loxocrambus sp. near **mojaviellus** Forbes

A somewhat heterogeneous assemblage of specimens from the low deserts of California has been designated as a new species with a manuscript name by A. B. Klots (AMNH). We accumulated large series of this species in a survey of active dune systems of the Colorado and Mojave deserts (Powell, 1978). Included was one specimen that remained unfed, presumably as a prepupal larva in diapause, for 28 months.

The larva was sifted from active dunes south of Rice, Riverside Co., CA, Jan. 30, 1977, by J. T. Doyen and P. A. Rude (JAP 77A19). In early February I opened its sand-covered silken tube to find a large pyralid larva. The larva evidently was fully fed and did not accept plants in the lab. It was retained in a dry container with sand in the mobile trailer lab (unheated 6 weeks in midwinter) until February, 1978, then in the outdoor cage at Berkeley for one year. Rainfall resulted in wetting the sand once or twice during the 1978–79 winter. After storage in the mobile trailer lab again for four months, a somewhat dwarfed male emerged 1 June, 1979.

GEOMETRIDAE

Eupithecia dichroma – johnstoni group

A single specimen of *Eupithecia* was reared after spending two winters in diapause, and although the species identification is questionable, the record is noteworthy because prolonged diapause has been recorded for few geometrids. The moth failed to expand its wings fully upon emergence, but it seems to match the description of *E. johnstoni* McDunnough with only minor differences. The latter species, which was known only from the type male from Inyo County, CA, at the time of McDunnough's revision in 1949, has the whitish ground color on the forewings more contrasting with the red-brown subbasal and subterminal bands than seems to be true of the deformed reared specimen from Modoc County, CA. The male genitalia, particularly the unique aedeagus, confirm a close association with *johnstoni* and *E. rindgei* McDunnough, a paler species described from Plumas County, CA. The cornutus is lightly sclerotized basally in the Modoc example, a feature not shown in McDunnough's (1949) illustrations, but otherwise the three species are quite similar in this character.

The geometrid caterpillar was collected incidentally along with larvae of *Pyramidobela quinquecristata* Braun (Ethmidae) and a polyphagous tortricid, *Sparganothis tunicana* (Walsingham), which were webbing and feeding on inflorescences of *Penstemon laetus* spp. *roezlii* (Scrophulariaceae) at Rock Creek, 15 km NE of Adin, Modoc Co., 12 June 1974 (JAP 74F21). Several adults of the *Pyramidobela* and *Sparganothis* were reared within a month; neither of these species diapauses as a prepupal larva or pupa. In late July I discovered a geometrid pupa in the material and placed it in a plastic vial with tissue paper. This was retained in the mobile trailer lab at Berkeley until mid-December, then transferred to the insectary at Russell for 60 days. Examination indicated the pupa to be still alive in August, 1975, and it was again moved to the Russell insectary for overwintering. It was transferred back to Berkeley on 14 March 1976, and the moth emerged 14 days later, after ca 21 months in diapause.

SATURNIIDAE

Hemileuca electra (Wright)

This fall-flying, diurnal species occurs in southern California, where the larvae feed on *Eriogonum fasciculatum* (Polygonaceae) in spring.

Summer is passed by pupae in diapause. As noted by Comstock & Dammers (1939), in captivity the larvae are susceptible to disease and are difficult to rear.

I collected seven mature larvae at Mission Gorge, San Diego Co., CA, [ca 8 km W of Santee] on *E. fasciculatum*, 19 March 1950. None successfully developed that season, but one pupa held indoors carried over, and a female eclosed 27 November 1951, after 20 months diapause. The capability of emerging following one summer of dormancy or delaying until the succeeding or a later autumn may be characteristic for all species of *Hemileuca*. It has been recorded for *H. maia* (Drury) (Ferguson 1971; W. D. Winter *in litt.*), *H. burnsi* Watson (Comstock and Dammers, 1937), *H. juno* Packard (Comstock & Dammers, 1939), and *H. eglanterina* (Boisduval) (Winter, *in litt.*) and inferred for others by Tuskes (1985).

Saturnia mendocino Behrens

This diurnal saturniid occurs in the North Coast Ranges and Sierra Nevada of California (Ferguson, 1972), south at least to El Dorado Co. (UCB specimen). The larvae have been recorded by several authors to feed on *Arbutus* and *Arctostaphylos* (Ericaceae); Ferguson suggests that *S. mendocino* also feeds on shrubs of other families, apparently based on circumstantial associations for the closely related species, *S. walterorum* Sala & Hogue, in southern California.

David Wagner collected an ovipositing female and egg cluster of *S. mendocino* on *Arctostaphylos pungens* var. *montana* near Alpine Lake, Marin Co., CA, during a field trip with our immature insects class, on April 13, 1979. The female continued to produce eggs for several days; larvae were reared, May 4 to July 3, 1979, on *Arctostaphylos* from the U. C. campus (DLW lot L10–14–79). The cocoons were held in an outdoor cage in a plastic bag with damp moss during the 1979–80 winter. Four adults emerged in May, 1980. The remaining pupae were left in a drawer at room temperatures, yet produced two more moths in 1981, none the following year, and one *S. mendocino* finally emerged in May, 1983, after nearly 4 years in diapause.

Third and fourth year emergence also is recorded in the Palearctic species, *Saturnia pyri* (Schiffermüller), in Maryland (Bryant, 1980).

NOTODONTIDAE

Pheosia rimosa Packard

I discovered two larvae of this widespread species at Rock Creek, ca 2 km SW of Tom's Place, Mono Co., CA, 26 August 1983, on *Populus trichocarpa* (Salicaceae) (JAP 83H122). The caterpillar, which I mistook for Sphingidae owing to the short caudal horn, was described by Dyar (1891) and others and illustrated in Packard's monograph, but its remarkable crypsis seems not to have been mentioned. The larvae are peculiar compared to most Notodontidae, being naked, gray, with a greasy or pearly sheen, prominent spiracles and exaggerated intersegmental constrictions. They perch during the day, hanging downward, on the stems of poplar, back of the distal leaves. There they resemble the older stems, which develop rings of enlarged nodal growth that are matched exactly in color by the larvae.

The collection was temporarily housed in a plastic bag and transported in a field ice box during a trip, and one of the larvae pupated loose in the bag by August 31. The larva, pupa and foliage were transferred to a plastic box with sandy soil September 1, but the lot was allowed to become moldy while stored in the mobile trailer lab at Berkeley, and the second larva died. In February, 1984, the material was still damp and the loose pupa on the soil surface was noted to have a thin bloom of mold on its surface and was presumed dead. It was placed in a refrigerator (± 4°C) for 5 weeks but did not metamorphose in that season.

The pupa was left in situ on the soil surface and was refrigerated during the 1984–85 winter, from October until February. A large, normally developed female of *P. rimosa*, which is of the pale morph characteristic of populations east of the Sierra Nevada in California, emerged during 16–23 March 1985, after 18 months in diapause. That is, nearly one year later than presumably would be normal for this bivoltine species.

NOCTUIDAE

Egira crucialis (Grote)

There appear to be few records of prolonged diapause in Noctuidae, although many overwinter as pupae. Thus carryover records of *Egira crucialis*, for which we do not have accurate emergence dates, seem worthy of recording, to call attention to the potential for extended dormancy in noctuids.

Species of *Egira* Duponchel (=*Xylomyges* Gn. and *Xylomania* Hamp.) are univoltine and fly in early spring, often at quite cold temperatures. In central California they are active from late December to May, the particular flight period varying with the species and elevation. Larvae feed during spring foliation, and pupae in diapause estivate and hibernate until midwinter or spring. We have reared only a few of them, but two *E. crucialis* remained in diapause beyond the normal spring flight period.

Evidently *Egira crucialis* is a general feeder; we found young larvae on new foliage of *Pseudotsuga menziesii* (Pinaceae), while previous records are from hardwoods. Crumb (1956) listed collections from *Alnus* (Betulaceae) and *Quercus* (Fagaceae) in Washington State, and Prentice (1962) recorded those plant genera as well as *Arbutus* (Ericaceae) and *Salix* (Salicaceae) from Vancouver Island, British Columbia. Our material was taken ca 2 km west of Angwin, Napa Co., CA, 15 May and 1 June, 1979 (DeBenedictis & Powell — JAP 79E62, 79E73). Larvae were reared in polyethylene bags, then transferred to translucent plastic boxes with sterile soil after ca 3 weeks. Pupae in soil-encrusted cells were transferred to the outdoor cage in December and held there until April, 1980. First-year adults should have emerged by this time because in this area *E. crucialis* flies from mid-February to early April. The collections were not given close surveillance after spring, 1980; they were stored in the mobile trailer lab, without heating for 6 weeks in midwinter. One dead female *E. crucialis* was found in the 79E73 lot in early April, 1981, and a dead male in 79E62 in June, 1982. The circumstances indicated that both emerged during the 1980–81 winter (i.e., after 18–22 months in diapause), while I was away on sabbatic leave, although the male may have held over an additional year.

Discussion

Previously unpublished instances of diapause extending one or more years beyond that believed to be normal in the population are reported for 19 species of moths, representing 8 superfamilies. Including these, Table 1 lists taxa for which I have seen records of prolonged diapause in 90 species in 10 superfamilies. This summary is incomplete but reflects the state of knowledge about the taxonomic distribution of the phenomenon in Lepidoptera. The preponderance of records in a few families, Prodoxidae, Saturniidae, Pieridae, and Papilionidae, at least in part indicates rearing efforts, while some taxa such as Geometridae and Noctuidae may be disproportionately underrepresented owing to the failure of lepidopterists to look for viable carryover individuals. It is no coincidence that most of the microlepidoptera listed in Table 1 are Prodoxidae and Ethmiidae, the two families with which I have worked most intensively.

While it would be premature to attempt a detailed summary of the pattern of occurrence of prolonged diapause in Lepidoptera, a few generalizations seem apparent: a) Dormancy persists beyond the normal flight season in prepupal larvae and pupae; it is rare or undetected in adults, eggs, and early instar larvae. b) It has been observed most often in cone- and seed-feeding species that depend upon fruit crops of erratic abundance and in Lepidoptera that live in areas of seasonal drought. c) The ability to carryover appears to be more prevalent among certain butterflies and larger moths than in smaller moths.

The generalization that prolonged diapause is more common in Macrolepidoptera may be a picture painted with too broad a brush; more likely the phenomenon is characteristic of certain taxa, and is rare in others, within most Ditrysian superfamilies. For example, in the Tortricidae, I have seen records of delayed emergence in 8 species, reported in 17 references by prior researchers, in addition to the one given here. All of these are seed-feeding Eucosmini (1 species) and Grapholitini (7 spp.) (Olethreutinae). Although biologies of a large number of Tortricinae have been studied, apparently prolonged diapause has been reported in none of them. Tortricinae generally and members of the dominant, worldwide tribe Archipini in particular, tend to be species that are indiscriminate in feeding preferences and life cycle pattern, often homodynamic with no fixed dormancy stage. Species that undergo diapause do so as eggs or first instar larvae or in adults; it is very rare in full grown larvae or pupae (Powell, 1964: 17). By contrast, most Olethreutinae are host specific (6% polyphagous vs. 24% in Tortricinae, Powell 1980) with a fixed life cycle, and dormancy commonly occurs in prepupal larvae. Not coincidentally, olethreutines, especially Eucosmini, reach their greatest diversity, while tortricines are depauperate, in desert areas.

On the basis of literature reports and the taxonomic diversity of prolonged diapause among my rather few rearings of desert species, I speculate that most oligophagous Lepidoptera in areas of seasonal drought estivate as prepupal larvae or pupae and that most if not all are capable of producing a facultative second flight and/or carrying over to a subsequent season. Because 2–3 year diapause can occur successfully in tiny moths, such as *Coleophora* in the Turkistan desert (Falkovitch, 1973), we may expect that in groups such as Gelechiidae, which are characteristically diverse in arid and semiarid regions, the capability of prolonged diapause is not rare. For such insects winter temperatures may be important mitigators of diapause development, as in yucca moths, but rainfall has been implicated as critical in some butterflies (e.g., Emmel, 1975:144, and unpubl. *in litt.*; Nakamura & Ae, 1977), as has been documented for various other insects.

Various aspects of diapause and its importance in insect seasonality have been extensively studied, but the physiological mechanisms of prolonged diapause are poorly understood (e.g., Tauber et al., 1986). Presumably particular token stimuli needed to promote the late phases of diapause maintenance and diapause termination are not received. Hence, when thermal or other thresholds are reached that would have resulted in postdiapause development, the diapause maintenance period continues. The degree of individual variation poses interesting, as yet unanswered questions; often some individuals metamorphose, while others exposed to the same stimuli do not. Usually this occurs in environmental conditions that are abnormal, but such variation indicates there are differing genetic factors in diapause potential within colonies, or even among sibs of one egg clutch.

Tauber et al. (1986: 53, 188, 198, 274) have reviewed the role of prolonged diapause in the evolution of seasonality, life histories and speciation. In their discussion there is an assumption which has been made by several authors that extended dormancy regularly occurs in a certain proportion of the population as an evolutionary bet-hedging tactic. Tauber et al. credit me with recognizing that there are two kinds of prolonged diapause, either a response by whole populations to adverse conditions by carrying over, or a normal, genetically determined occurrence in a certain proportion of the individuals (Powell, 1974). However, I also pointed out that we do not have experimental evidence to demonstrate that there is a fixed polyphenic expression of the genotype, wherein a small number of individuals carry over irrespective of environmental conditions as a kind of buffer against extraordinary climatic extremes. This is still true; in Lepidoptera we do not have data to document that populations of any species express this phenomenon.

In yucca moths (*Prodoxus*) I have convincing evidence that such genetic predisposition is not the case; under optimum winter environments all or nearly all larvae undergo development, while in adverse conditions all or nearly all maintain diapause (Powell, 1984a, b, 1985). Multiannual emergence patterns such as reported by Carolin (1971) for *Coloradia* (Saturniidae) appear to represent a fixed polyphenism, but that kind of genetic variability may be manifested only in response to suboptimal climatic situations. Hence, there may not be two discrete classes of prolonged diapause. Rather, populations adapted to erratically variable seasonal and biotic environments may be composed of genetically differing individuals such that none, few, many or all maintain diapause depending upon the degree of fitness to optimum seasonal conditions. With *Prodoxus* it is easy to obtain 100% carryover but almost impossible to promote 100% diapause development under experimental circumstances in the first year. Later, after several years in diapause, individuals will respond to environmental cues that were not sufficient in the first year and proceed through development. This kind of response, rather than a genetically predisposed calendar of events that occurs irrespective of external stimuli, may be producing successive year emergence observed in other insects.

Lepidopterists are urged to record observations such as those given here, particularly the environmental conditions to which dormant stages are subjected, as a necessary step toward more detailed analysis of prolonged diapause.

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